

the New England Fishery Management Council elected to defer most of the cuts indicated for 2012 and 2013 until the second half of 2013. The socioeconomic adjustment coupled with the two warmest years on record led to fishing mortality rates that were far above the levels needed to rebuild this stock.

The impact of temperature on Gulf of Maine cod recruitment was known at the start of the warming period (20), and stock-recruitment model fit to data up to 2003 and incorporating temperature produces recruitment estimates (Fig. 2A, yellow diamonds) that are similar to the assessment time series. Ignoring the influence of temperature produces recruitment estimates that are on average 100% and up to 360% higher than if temperature is included (Fig. 2A, gray squares). According to a simple population dynamics model that incorporates temperature, the spawning stock biomass that produces the maximum sustainable yield (SSB_{msy}) has been declining steadily since 2002 (Fig. 3) rather than remaining constant, as currently assumed. The failure to consider temperature impacts on Gulf of Maine cod recruitment created unrealistic expectations for how large this stock can be and how quickly it can rebuild.

We estimated the potential for rebuilding the Gulf of Maine cod stock under three different temperature scenarios: a “cool” scenario that warms at a rate of $0.02^\circ \text{ year}^{-1}$; a “warm” scenario that warms at $0.03^\circ \text{ year}^{-1}$, the mean rate from climate model projections; and a “hot” scenario that follows the $0.07^\circ \text{ C year}^{-1}$ trend present in the summer temperature time series. If fishing mortality is completely eliminated, populations in the cool and warm scenarios could rebuild to the temperature-dependent SSB_{msy} in 2025, slightly longer than the 10-year rebuilding timeline established by U.S. law, and the hot scenario would reach its target 1 year later (Fig. 3). Allowing a small amount of fishing ($F = 0.1$) would delay rebuilding by 3 years in the cool and warm scenarios and 8 years in the hot scenario. Note that estimating SSB_{msy} without temperature produces a management target that may soon be unachievable. By 2030, a rebuilt fishery could produce more than 5000 mt year^{-1} under the warm scenario, a catch rate close to the average for the fishery for the previous decade. Under the hot scenario, the fishery would be 1800 tons year^{-1} —small, but potentially valuable. Thus, how quickly this fishery rebuilds now depends arguably as much on temperature as it does on fishing. Future management of Gulf of Maine cod would benefit from a reevaluation of harvest control rules and thorough management strategy evaluation of the application of temperature-dependent reference points and projections such as these.

As climate change pushes species poleward and reduces the productivity of some stocks, resource managers will be increasingly faced with trade-offs between the persistence of a species or population and the economic value of a fishery. Navigating decisions in this context requires both accurate projections of ecosystem

status and stronger guidance from society in the form of new policies. Social-ecological systems that depend on a steady state or are slow to recognize and adapt to environmental change are unlikely to meet their ecological and economic goals in a rapidly changing world.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/350/6262/809/suppl/DC1
Materials and Methods
Figs. S1 to S6
Tables S1 to S5
References (27–35)

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EXTINCTION EVENTS

Body-size reduction in vertebrates following the end-Devonian mass extinction

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Following the end-Devonian mass extinction (359 million years ago), vertebrates experienced persistent reductions in body size for at least 36 million years. Global shrinkage was not related to oxygen or temperature, which suggests that ecological drivers played a key role in determining the length and direction of size trends. Small, fast-breeding ray-finned fishes, sharks, and tetrapods, most under 1 meter in length from snout to tail, radiated to dominate postextinction ecosystems and vertebrate biodiversity. The few large-bodied, slow-breeding survivors failed to diversify, facing extinction despite earlier evolutionary success. Thus, the recovery interval resembled modern ecological successions in terms of active selection on size and related life histories. Disruption of global vertebrate, and particularly fish, biotas may commonly lead to widespread, long-term reduction in body size, structuring future biodiversity.

Body size plays a crucial role in life histories, affecting generation times, energy demands, and population sizes (1, 2). Size increases (Cope’s rule) are thought to define Phanerozoic biodiversity, resultant from coordinated active trends, preferential survival of larger-bodied forms (lineage sorting), or passive diffusion (2–4). In contrast, the Lilliput effect—that is, temporary size reduction after mass

extinction—is supported by few observations and remains under dispute (4, 5). This effect is widely considered a passive result of extinction

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selectivity or taphonomic bias (4, 5). Global, long-term size reduction has not been proposed or reported following mass extinction (4). Persistent shrinkage has been restricted to specialized groups—such as birds, plankton, or island faunas (6–9)—in normal times.

Devonian-Mississippian [419 to 323 million years ago (Ma)] vertebrates were the first to exhibit modern ranges of body size (10–12), jaw and body forms (5, 13), diet (5, 14), and biodiversity (5, 15). Their diversification was coincident with dramatic temperature and atmospheric oxygen changes (11, 16, 17). The mid-Paleozoic vertebrate record is thus an ideal test case for body-size phenomena. Limited samples of Paleozoic marine fishes have been used to link size increases with atmospheric oxygen rises (2, 10, 11), despite the

lack of a physiological mechanism (5). Yet, Phanerozoic (especially Paleozoic) vertebrate size data remain poorly sampled (2, 5, 10–12, 18).

The Paleozoic vertebrate record is divided by the Hangenberg event (359 Ma), arguably the most severe mass extinction for this group (5, 13–15) (fig. S1). This event involved the loss of 11 of 22 major jawed vertebrate clades (corresponding to orders) and >96% of species (19) and also entailed ecosystem restructuring (5, 13–15). The end-Devonian event should have affected size distributions as a correlate of other ecological traits (1). Yet, there are no hypotheses or comprehensive data sets for vertebrate size change across the event, just as these are lacking for other extinctions (5). This is a glaring oversight, considering the current declines in fish popula-

tions, especially larger-bodied forms (18), and the need for predictions of long-term effects.

We assembled a database of 1120 body lengths (in centimeters) for Devonian-Mississippian vertebrates (20) (tables S1 and S2); our database contains the vast majority of named species from all biomes (fig. S1). Using log-transformed sizes binned by stage (1326 points) (table S3), we found that Devonian vertebrates exhibited persistent stepwise size increases [ordinary least squares (OLS) and reduced major axis (RMA) regressions $P = 0.0001$, $r = 0.45$] (Fig. 1A, figs. S2 to S8, and tables S4 and S5) in line with Cope's rule predictions (2–4). In contrast, vertebrates exhibited persistent body-size reduction over the Mississippian (OLS and RMA $P = 0.0001$, $r = -0.25$) (tables S2 to S5; Fig. 1A; and figs. S3, S4, and S6), with significant differences between distributions in subsequent stages (Mann-Whitney U test; Tournaisian versus Viséan: $P = 0.0041$; Viséan versus Serpukhovian: $P = 0.018$) (table S6). This finding supports the notion of global shrinkage in vertebrates after the end-Devonian extinction, a prolonged Lilliput effect or reverse Cope's rule (4).

Prolonged shrinkage could result from cumulative short-term Lilliput effects after repeated abiotic events (4). However, although glacial aftereffects occurred during the early recovery interval, the Mississippian was more abiotically stable than the later Devonian (17, 18, 21). There is no evidence for further vertebrate turnover linked with perturbations (5, 13–15). We fit multiple conflicting temperature and oxygen models to determine whether our data supported climate-based hypotheses for size change (tables S7 to S12). Contrary to energetics-based assumptions (2, 10, 11), vertebrate sizes were negatively correlated with one oxygen model (GEOCARBSULFvolc; $P = 0.0001$, $r = -0.33$) (18) yet showed no relationship with the others (tables S9 to S11). Contrary to Bergmann's rule that size is negatively influenced by temperature (4), vertebrate sizes were positively correlated with one sea surface temperature proxy (δO_{18} sea surface; $P = 0.0001$; $r = 0.020$) (16) yet showed no relationship with other estimates (tables S7 to S9).

To determine the exact drivers of our divergent size patterns, we fit active trend (directional change), random walk, and stasis models alongside the best-fit oxygen and temperature estimates (16, 17). An active trend with a shift centered on the end-Devonian event was overwhelmingly supported [359 Ma; Akaike weight (AW): 0.93] (table S13). Thus, vertebrate size change was driven by active selection stemming from biotic factors and/or long-term conditions, which suggests that relationships with climatic change and smaller abiotic events were incidental (11).

To determine whether preservational biases affected overall patterns, we analyzed size structure for well-sampled faunas (Fig. 2A and table S14). Large vertebrates (>80 cm in body length) were overrepresented in Late Devonian ecosystems (Figs. 2A and 3A and tables S12 to S16). Thus, global patterns mirrored local trends. Faunas from after the extinction, particularly those during "Romer's Gap" (359 to 331 Ma) (5, 16), showed

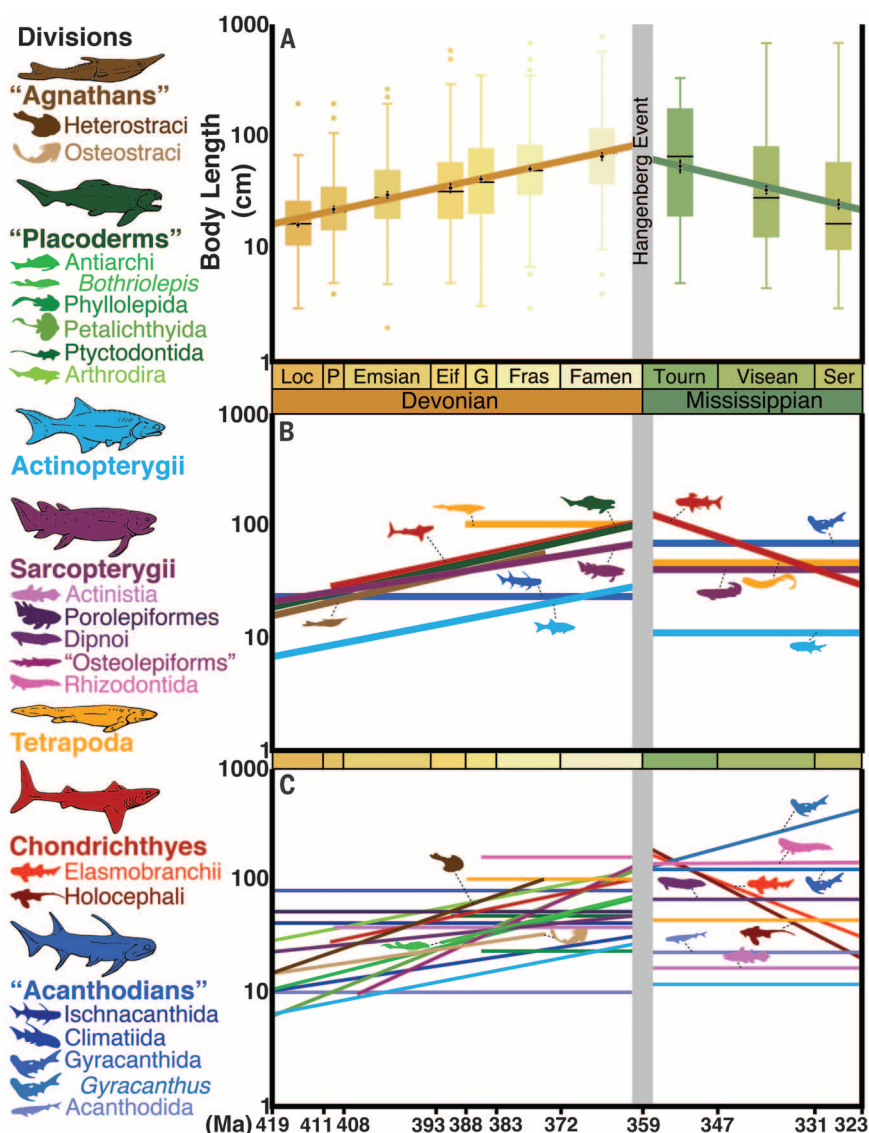


Fig. 1. Vertebrates experienced body-size reduction after the Hangenberg extinction. (A) Stage distributions and OLS trend lines for the Devonian and Mississippian. Black dots represent means; lines represent variance. Loc, Lochkovian; P, Pragian; Eif, Eifelian; G, Givetian; Fras, Frasnian; Famen, Famennian; Tourn, Tournaisian; Ser, Serpukhovian. (B) Trend lines for major vertebrate divisions. Flat lines represent the mean length for groups with insignificant effect sizes. (C) Trend lines for vertebrate subclades.

severe losses among larger size classes, despite similar numbers of species (analysis of similarity, $P = 0.009$) (table S15 and Fig. 2A). The majority of

taxa at early Mississippian sites were under 40 cm in length, similar to early Devonian faunas dominated by jawless fishes (tables S16 to S18;

Figs. 2, B and C, and 3, B to D; and figs. S14 and S15). Altered size structure is indicative of an ecosystem-wide Lilliput effect.

To test the depth of our observed size trends, we analyzed six vertebrate divisions and 22 widespread clades. We aimed to reveal whether the overall pattern resulted from coordinated change, lineage sorting, or taxonomic sampling bias (Fig. 1B) (2, 3). All well-sampled Devonian lineages exhibited significant size increases, including the dominant placoderms and lobe-finned fishes (Sarcopterygii) (tables S19 and S20, Fig. 1B, and figs. S18 to S21) and widespread genera such as *Bothriolepis* (tables S25 and S26, Fig. 1C, and figs. S40 and S41). Multivariate model-fitting strongly supported an active coordinated trend (AW: 0.99) (tables S22 and S31). Therefore, rather than wholly resulting from emerging dominance of novel, already-large-bodied groups (lineage sorting), Devonian vertebrate size increases largely occurred within ecomorphologically stable lineages (2, 10–12). This finding supports a traditional Cope's rule phenomenon (2–4) and validates the signal in our complete data set.

On average, any postextinction lineages started out smaller than their latest Devonian forebears (Fig. 1), a classic Lilliput effect (4). However, reduced sizes also characterized newly dominant forms—including cartilaginous and ray-finned fishes and tetrapods (Chondrichthyes, Actinopterygii, and Tetrapoda)—for the next 36 million years (5, 13–15) (tables S32 and S33; Fig. 1; and figs. S68 to S70, S74, and S75). This resulted from active trends (e.g., Chondrichthyes), downward shifts in size distribution (e.g., Actinopterygii) (table S21), and/or stasis (e.g., Tetrapoda) (table S19). Newly genus-poor clades (5, 15) exhibited size patterns that conflicted with the overall decline. Some groups (e.g., Rhizodontida) maintained their Devonian body sizes despite diversity losses (15) (Fig. 1C, table S1, and figs. S36 and S37). Others, such as the Acanthodida and Dipnoi (Fig. 1C and tables S26 to S30), showed marked length increases across the boundary. The giant acanthodian *Gyracanthus* even exhibited a trend toward larger sizes (Fig. 1C, figs. S80 and S81, and table S27). These forms have previously been dubbed “dead clades walking” (5, 15) to indicate that they are survivors marked by low, declining diversity (22).

The existence of large, marginal survivors reduced effect size (tables S4 and S5) by adding long tails to Mississippian size distributions (table S3 and Fig. 1A). Tournaisian mean body length remained similar to that for the Famennian, despite reductions in all other metrics (tables S3 and S6 and Fig. 1A). This masked an immediate Lilliput effect at the faunal level, where small (<40 cm) speciose actinopterygian and chondrichthyan taxa made up an increasing majority of taxa (15) (tables S14 to S17). Maximum body lengths were actually greater in the Mississippian than in the Devonian (Fig. 1A and table S3). These values alone would give a false impression of continued Cope's rule trends (2, 11, 12).

Postextinction global shrinkage was underlain by differential diversification and extinction (23),

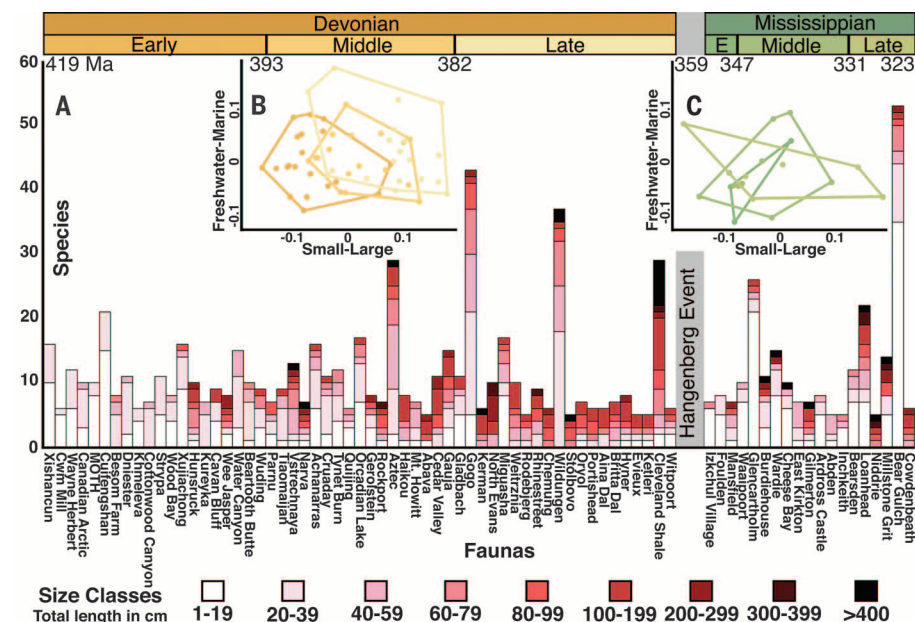
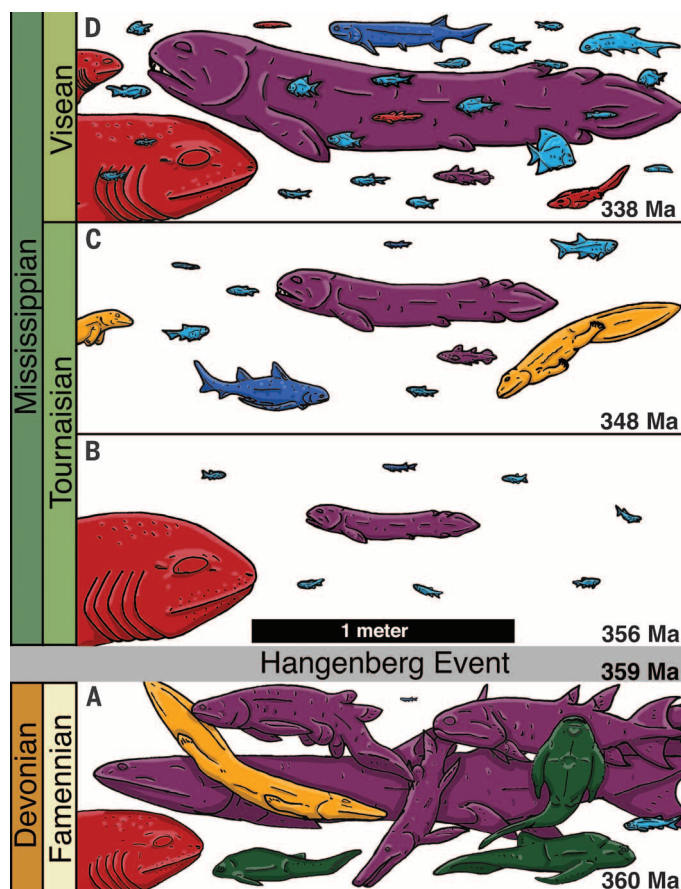


Fig. 2. Small vertebrates were dominant in postextinction faunas. (A) Histogram of species per fauna. (B) Nonparametric multidimensional (NMDS) ecospace plot of Devonian faunas binned by interval. (C) NMDS ecospace plot of Mississippian faunas binned by interval.

Fig. 3. Small vertebrates were increasingly diverse in postextinction ecosystems. Represented faunas include taxa with known body sizes from elsewhere in the same region and time bin. See Fig. 2A and tables S1 and S14 for sizes and Fig. 1 for taxon key. (A) Andreyevka-2, Russia. (B) Andreyevka-1/Izschul Village, Russia. (C) Foulden, Scotland. (D) Glencartholm, Scotland.



species selection, and active trends within lineages (24). Larger vertebrates comparable to our “dead clades,” such as Devonian placoderms and extant sharks (25), tend to have low fecundity, high parental investment, and increased energy demands balanced by long life spans, multiple breeding seasons, and wide habitat ranges (*K*-selection) (1). Extremes of these traits may confer relative extinction resistance in ecologically depleted times while limiting the potential for speciation (26–28). Smaller vertebrates, such as holocephalans and ray-finned fishes (29), tend to have high reproductive rates, short generation times, and large populations (*r*-selection) (1). These traits may increase survival through sheer numbers while promoting diversification via higher variation and population fragmentation (24, 26).

The Mississippian recovery interval favored extreme life histories among survivors, selecting for a bimodal size distribution. In the longer term, larger-bodied but less speciose lineages, such as rhizodonts, remained marginal or went extinct (5, 16). Smaller-bodied, rapidly radiating lineages, such as ray-finned fishes, spread to dominate ecosystems (13, 16). Significant downward shifts in Mississippian chondrichthyan and actinopterygian size distributions suggest that this pattern was mirrored within groups (table S21). The Mississippian approximated a scaled-up ecological succession, in which small, short-lived taxa dominate, whereas larger, longer-lived forms are marginal (30).

Scattered observations suggest that this pattern is common during long-term recovery intervals. Gigantic, rare postextinction vertebrates were taken as a sign of ecological restoration (31). Shrinkage within postextinction invertebrates (4, 6, 8) was considered restricted or temporary. The oft-noted tendency for major clades to descend from smaller taxa may be linked to such characteristics of postextinction radiations (3, 7). New, diversifying modern ray-finned fishes were smaller than older, diminished ray-finned fish lineages in the Triassic (32). Thus, size-related selection has likely shaped vertebrate biodiversity.

Small, opportunistic taxa eventually give way to larger, longer-lived forms in disturbed ecosystems (29). Likewise, Cope's rule trends may be favored during stable, saturated times at some distance from recovery conditions (2, 5, 26, 27). This describes the intervals containing Devonian vertebrates, late Mesozoic giants, and later Cenozoic mammals (2, 5, 27). An overall Phanerozoic Cope's rule (2) could result from a greater number and length of stable nonrecovery intervals. Vertebrate size trends appear to result from active selection, probably on life histories, with direction based on long-term conditions and survival.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S91
Tables S1 to S40
References (33–49)

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SMALL RNAs

MicroRNA-encoded behavior in *Drosophila*

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The relationship between microRNA (miRNA) regulation and the specification of behavior is only beginning to be explored. We found that mutation of a single miRNA locus (*miR-iab4/iab8*) in *Drosophila* larvae affects the animal's capacity to correct its orientation if turned upside down (self-righting). One of the miRNA targets involved in this behavior is the *Hox* gene *Ultrabithorax*, whose derepression in two metameric neurons leads to self-righting defects. In vivo neural activity analysis reveals that these neurons, the self-righting node (SRN), have different activity patterns in wild type and miRNA mutants, whereas thermogenetic manipulation of SRN activity results in changes in self-righting behavior. Our work thus reveals a miRNA-encoded behavior and suggests that other miRNAs might also be involved in behavioral control in *Drosophila* and other species.

The regulation of RNA expression and function is emerging as a hub for gene expression control across a variety of cellular and physiological contexts, including neural development and specification. Small RNAs such as microRNAs (miRNAs) (1) have been shown to affect neural differentiation (2, 3), but their roles in the control of behavior are only beginning to be explored.

Previous work in our laboratory focused on the mechanisms and impact of RNA regulation

on the expression and neural function of the *Drosophila Hox* genes (4–7). These genes encode a family of evolutionarily conserved transcription factors that control specific programs of neural differentiation along the body axis (8–10), offering an opportunity to investigate how RNA regulation relates to the formation of complex tissues such as the nervous system.

We used the *Hox* gene system to investigate the roles played by a single miRNA locus (*miR-iab4/iab8*) (4, 11–16) on the specification of the nervous system during early *Drosophila* development. This miRNA locus controls the embryonic expression of posterior *Hox* genes (4, 11–16). Given that we found no detectable differences in the morphological layout of the main components of the

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Body-size reduction in vertebrates following the end-Devonian mass extinction

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The small will inherit the Earth...

Understanding how communities and ecosystems recovered from the previous five global extinction events sheds light on how extinctions shape broad patterns of biodiversity. Sallan *et al.* looked across vertebrate species during and after the Devonian extinction (see the Perspective by Wagner). Small-bodied species, with rapid reproductive rates, dominated post-extinction communities, despite the presence of many successful large-bodied species before the extinction. This pattern mimics, to some degree, current patterns of extinction, suggesting that we might expect similar loss of large-bodied species if we continue along our current path.

Science, this issue p. 812; see also p. 736

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